TITLE: ANTHROPOGENIC INFLUENCES ON PRIMATE ANTIPREDATOR BEHAVIOR AND IMPLICATIONS FOR RESEARCH AND CONSERVATION

RUNNING TITLE: HUMAN INFLUENCE ON PRIMATE ANTIPREDATOR BEHAVIOR

AUTHORS: Laura R. LaBarge[1,2], Russell A. Hill[2,3,4], Carol M. Berman[1,5], Susan W. Margulis[6,7], Andrew T. L. Allan[2,3]

[1]Program in Evolution, Ecology and Behavior, The State University of New York at Buffalo, Amherst, NY, USA

[2]Primate and Predator Project, Lajuma Research Centre, Louis Trichardt, South Africa

[3]Department of Anthropology, Durham University, Dawson Building, South Road, Durham DH1 3LE, UK

[4]Department of Zoology, University of Venda, Private bag X5050, Thohoyandou 0950, South Africa

[5]Department of Anthropology, The State University of New York at Buffalo, Amherst, NY, USA

[6]Department of Animal Behavior, Ecology and Conservation, Canisius College, Buffalo, NY, USA

[7]Department of Biology, Canisius College, Buffalo, NY, USA

Corresponding Author: Laura R. LaBarge, 380 MFAC Department of Anthropology, The State University of New York at Buffalo, Amherst, NY, USA, 14260

lauralab@buffalo.edu

ABSTRACT: Predation risk affects prey species behavior, even in the absence of a direct threat, but human-induced environmental change may disturb ecologically significant predator-prey interactions. Here we propose various ways in which knowledge of antipredator tactics, behavioral risk effects, and primate-predator interactions could assist in identifying human-caused disruption to natural systems. Using behavior to evaluate primate responses to ongoing environmental change should be a potentially effective way to make species conservation more predictive by identifying issues prior to more dramatic population declines. A key challenge here is that studies of predation on primates often use data collected via direct observations of habituated animals and human presence can deter carnivores and influence subjects' perception of risk. Hence, we also review various indirect data collection methods to evaluate their effectiveness in identifying where environmental change threatens wild species, while also minimizing observer bias.

keywords: antipredator behavior, primate, human-shield effect, conservation, human-induced rapid environmental change (HIREC)

## INTRODUCTION

Predators influence their prey through both direct consumption and non-lethal "risk effects" on plastic phenotypic traits (Moll et al. 2017; Preisser, Bolnick, & Benard, 2005). In particular, the behavioral consequences of risk have received much attention from ecologists in recent decades (Creel & Christianson, 2008; Moll et al. 2017; Preisser et al. 2005). When prey animals perceive themselves to be under high risk, their responses can carry foraging and physiological costs that affect individual reproductive success (Creel et al. 2007; Creel & Christianson, 2008). These costs can scale up to influence overall population density and demographics (Atkins et al. 2019; Creel et al. 2007; Creel & Christianson, 2008) and produce

cascading effects on the wider ecosystem (Atkins et al. 2019; Laundré et al. 2010). Despite the well-recognized importance of perceived risk in shaping prey behavior and ecology, the idea that fear as an emotional state can drive animal decision-making is relatively new in ecology (Brown, Laundré, & Gurung, 1999; Laundré, et al. 2010). This contrasts with psychological research on non-human primates that has long acknowledged the importance of fear (e.g. Joslin, Fletcher, & Emlen, 1964). Yet, in comparison to other mammalian taxa, relatively few studies of primates have focused on non-lethal risk effects (Bidner, 2014). As such, we lack a thorough understanding of how predation risk shapes their behavior and ecology. This knowledge is important because anthropogenic change is known to be a major driver of the way prey animals perceive and respond to risk (Berger, 2007; Sih, Ferrari, & Harris, 2011).

Human-induced rapid environmental change (hereafter HIREC: Sih et al. 2011) including habitat modification, fragmentation, over-exploitation, and the introduction of novel species can disrupt natural predator-prey relationships important to the integrity of ecological communities (Kareiva, 1987; Michalski & Peres, 2005). HIREC can obscure whether observed behaviors might be adaptive under a range of natural contexts or are more narrowly the result of plastic responses to specifically anthropogenic landscapes. Evidence indicates that species-typical predation rates in degraded or fragmented habitats could lead to primate extinction because predator and prey range overlap can increase when habitat loss causes both to be constrained to smaller areas (e.g., Irwin, Raharison, & Wright, 2009). Similarly, urbanization and fragmentation can concentrate less human-tolerant species in smaller natural areas, leading to more frequent interactions with predators (Parsons et al. 2019). Human hunting can also be thought of as a form of predation that threatens primate persistence as it can cause population declines even in continuous habitats, which is uncommon for other predators (Estrada et al. 2017; Reed & Bidner

2004). Yet, whether fear of humans might result in behavioral "risk effects" in wild primates is relatively uncertain (Bidner, 2014). In other taxa, fear of hunters can lead to changes in movement and habitat use that affect foraging decisions (Lone et al. 2014), not only in prey species but also apex predators (Ngoprasert, Lynam, & Gale, 2007; Ordiz et al. 2011). Exacerbating these problems are primates' relatively low reproductive rates and general inability to compensate for heightened levels of predation or hunting (Hill & Dunbar, 1998; Peres, 1990). Finally, because HIREC disproportionately affects large carnivores (Valeix et al. 2012), it is relatively unknown how the loss of these species and decreased prey risk perception would affect wider ecological communities (Bidner, 2014).

Research on behavioral indicators of risk perception in primates should be useful for identifying situations in which HIREC has caused disturbance to predator-prey relationships and where habitats or human activities need to be managed (Caro, 2016; Wong & Candolin, 2015). Within primates, these behaviors often include alarm calling upon detecting danger (Stanford, 2002), choosing to utilize safer habitats at the expense of riskier but more resource-rich locations (Coleman & Hill 2014; Cowlishaw, 1997; Willems & Hill, 2009), and monitoring the surrounding environment more intensely when/where they perceive more risk (Caro, 2005; Campos & Fedigan, 2014). Direct observation of habituated subjects is a commonly used method in field primatology (Williamson & Feistner, 2003) and these methods have looked for associations between antipredator behaviors and known risks from predators (Campos & Fedigan, 2014; Coleman & Hill 2014; Willems & Hill, 2009). It is also possible to use these same behaviors as indicators of fear with information on conflict/hunting risk from humans (Bryson-Morrison et al. 2017; Lindshield et al. 2017). Yet, direct observation also potentially biases antipredator studies because many carnivores actively avoid proximity to humans

(Boesch, 1991; Isbell & Young, 1993; Smith et al. 2017; Van Cleave et al. 2018). When comparatively tolerant prey species can perceive and exploit this increase in safety near observers or even human infrastructure, it is known as the "human-shield effect" (Berger 2007; Sarmento, & Berger, 2017). Evidence suggests that at least some primates do perceive an increase in safety while under observation (Nowak et al. 2014). Consequently, methods that reduce or eliminate the possibility of a "human-shield" are important both for more accurately identifying where HIREC has altered predator-primate relationships and for understanding the basic behavioral ecology of wild primates (Figure 1, Figure 2).

Broader questions of how habitat change might affect predator-primate interactions and co-occurrence can be asked using data collected from remote sensing technologies like Global Positioning System (GPS) collars (Fehlmann et al. 2017), and wildlife-triggered camera traps (Boyer-Ontl & Pruetz, 2014; Farris et al. 2014) that do not require habituation. Coupling behavioral data with information on predator diets through scat analysis can also be useful for identifying predation by elusive carnivores that may be difficult to observe (Brockman et al. 2008; Irwin et al. 2009). Field experiments using sensory cues from human hunters can indicate whether groups are subjected to hunting (Cagni et al. 2011) without requiring habituation to observers. Responses to experimental predator cues can additionally indicate whether predator-naïve primates recognize dangerous cues prior to a reintroduction program (Gil-da-Costa et al. 2003).

Other methods that do not require habituation include flight initiation distance (FID) experiments that record the distance at which a prey animal will flee from an approaching threat (Cooper & Frederick, 2007). These experiments can be used as both a general indicator of risk perception and as an indicator of hunting pressure (when used with an approaching human) by

comparing the response of animals in well-protected areas to those in locations that might be experiencing poaching or hunting (Donadio & Buskirk, 2006). Finally, the widely used method of giving-up density (GUD) experiments, in which researchers manipulate the amount of food in a foraging patch to indicate trade-offs between foraging and other activities, has been used to identify differences in perceived risk between habitats (Bedoya-Perez et al. 2013). Animals are predicted to cease foraging earlier and leave more food behind in risky habitats than in safer areas. Results of these experiments can provide indirect evidence that anthropogenic change alters risk perception (Nowak et al. 2016a; 2016b).

Critically assessing which methods are best for minimizing anthropogenic bias is important both for researchers studying fundamental behavioral biology (Caro & Sherman, 2011; Hockings et al. 2015) and for those aiming to conserve wild species. In this review we discuss some of the ways in which primate antipredator behaviors might be used to assess human impacts on wild populations. We also contrast available methodologies with the goal of highlighting those most useful for understanding adverse anthropogenic disturbance.

## METHODS

We conducted extensive literature searches between December 2017–2018 on Google Scholar and Web of Knowledge using combinations of derivatives of the terms: *predator/predation, anti-predator, risk, prey, habitat, carnivore,* and *primate* with the aim of investigating the most common methods for studying predation on primates. We also aimed to assess whether researchers used knowledge of antipredator strategies for conservation or for identifying where populations might be suffering from HIREC. Therefore, these searches were then repeated with derivatives of the terms: *human, anthropogenic, conservation, threatened, extinct,* and *hunt.* Finally, we noted the methods used in these studies and repeated our searches

with combinations of the terms: *vigilance, alarm call, experiment, playback, predator cue, Global Positioning System (GPS), remote sense, camera trap,* and *predator diet.* We also examined the references cited by each study as well as review articles on relevant topics (e.g. Allan & Hill, 2018; Bidner, 2014; Boinski, Treves, & Chapman, 2000; Fichtel, 2012; Isbell, 1994; Janson, 1998; Stanford, 2002) but did not include reviews, meta-analyses, simulation studies, or published abstracts in the total. We excluded papers where researchers studied a presumed antipredator behavior when the focus of the study was the risk of infanticide or within-species competition (e.g. vigilance and social monitoring). We additionally noted while reading these studies whether research was conducted on subjects habituated to humans and plotted these data to infer whether this practice might be declining with new remote sensing technologies (GPS/radio collars, camera traps etc.) or other methods that do not require direct observation. We expect our results are representative but not exhaustive of the primate predation literature. A limitation of this search is that wildlife managers may not publish reports on their activities in academic journals, and thus we may not have included relevant examples from non-peer-reviewed sources.

## RESULTS

In total, we found 222 studies focused on primate antipredator behaviors published between 1977 and 2018. Most of the studies (188/222) used direct observation of subjects that were tolerant of human presence (~85%) but the proportion using direct observation declined over time (Figure 3). Several recent studies used alternative methods including GPS data from collared primates and/or their predators (Adams & Kitchen, 2018; Bidner, Matsumoto-Oda, & Isbell, 2018; Isbell & Bidner, 2016; Isbell et al. 2018), camera traps (Boyer-Ontl & Pruetz, 2014; Farris et al. 2014; Isbell & Bidner, 2016), or predator scats for dietary analysis (Dollar,

Ganzhorn, & Goodman, 2007; Irwin et al. 2009; Jooste et al. 2012; Lenz & dos Reis, 2011; McGraw, Cooke & Shultz, 2006; Shultz et al. 2004; Shultz & Dunbar, 2006). For example, Isbell et al. (2018) were able to identify encounters between GPS-collared predators and primates without human interference using predator and prey spatial coordinates to determine when and where species interacted. Camera traps also allowed researchers to collect behavioral data without direct observation (Boyer-Ontl & Pruetz, 2014; Farris et al. 2014). Finally, predator diets, coupled with knowledge of species-typical antipredator traits, enabled researchers to identify characteristics that increase vulnerability to predation (Shultz et al. 2004). These studies tended to cite potential bias or interference from human observers as a reason for using these types of data, but none of them explicitly tested predictions about a "human-shield effect" that has been more extensively investigated in other taxa.

Field experiments also tended to keep human observers out of sight from subjects while using playbacks of predator sounds, visual predator cues, or artificial foraging patches (Arnold & Zuberbühler, 2006; 2013; Emerson & Brown, 2012; Emerson, Brown, & Linden, 2011; Makin et al. 2012). Predator experiments using sensory cues (visual models, playbacks, etc.) were the most common type of experiment, while a smaller number of more recent studies made use of giving-up densities (GUD) and one used flight initiation distance (FID) (Figure 4).

Of the total 222, 21 studies (~9.45%) were explicitly designed to address HIREC or species conservation (Table 1). Bryson-Morrison et al. (2017) and Lindshield et al. (2017) used direct observation of western chimpanzees (*Pan troglodytes verus*) to assess whether fear of humans might drive habitat use or foraging decisions. Specifically, Bryson-Morrison et al. used information about habitat-level differences in risk and examined whether this corresponded with utilization and activity budgets. The authors found that animals preferred to forage further from

potentially risky cultivated fields but did not actively avoid roads or human paths where the risk of conflict was high. Lindshield et al. also used direct observation but measured feeding rates and vigilance behaviors along with information on food availability. They found that subjects tended to react fearfully to the immediate presence of locals and increased their party size in anthropogenic habitats, although location-specific variation in risk did not seem to predict the likelihood of using a particular feeding patch. In both cases it is uncertain whether habituation to observers could have resulted in decreased fearfulness of other humans. We also included in this category studies by Teelen (2008) and Watts and Amsler (2013). While not explicitly related to humans, these studies used data from direct observation of chimpanzee hunting to investigate whether this natural predatory behavior could be unsustainable for their preferred primate prey and were thus relevant to conservation.

Studies relevant to conservation or HIREC also included those using remotely sensed data. Fehlmann et al. (2017) used GPS collars on adult male baboons living near Cape Town, South Africa, where rangers employed by the city actively deter baboons looking for anthropogenic food sources in urban areas or farms. Baboon activity levels (measured via attached accelerometers) were much higher in areas where the risk of being chased by a ranger was high. Brockman et al. (2008) and Irwin, Raharison, & Wright (2009) combined lemur behavioral data with information on predator diet selection using scats. Brockman et al. specifically focused on exotic predators and found evidence that they were feeding on wild lemurs, while Irwin et al. found evidence that fragmentation might put lemurs at risk of local extinction through predation. Finally, Farris et al. (2014) used camera traps to monitor lemur-predator co-occurrence across a variety of habitat types with varying levels of fragmentation. The authors found that introduced predators and humans were more active in fragmented forests

compared with continuous forests, whereas lemurs and native predators more active in continuous habitat.

Thirteen of the 21 studies that focused on HIREC/conservation used field experiments. These included simulated threats from hunters to gauge if antipredator behaviors towards humans could provide information on hunting pressure (Bshary 2001; Croes et al. 2007; Papworth, Milner-Gulland, & Slocombe, 2013), and all three found evidence in support. Four studies used artificial foraging patches in the form of giving-up density (GUD) experiments to investigate how human presence or human activities could affect primate risk perception (Nowak et al. 2014; 2016a; 2016b; 2017). Nowak et al. (2016a and 2017) found evidence that samango monkey (*Cercopithecus albogularis*) foraging behavior was sensitive to anthropogenic risk. GUD experiments in a more natural habitat conducted following samango live trapping indicated that habituated animals were unlikely to show a sustained fear response to researcher equipment once trapping was complete (Nowak et al. 2016b). Habituated subjects also tended to forage more on the ground from GUD patches, indicating that observers might decrease subjects' perception of risk from terrestrial predators (Nowak et al. 2014). One study attempted to measure variation in risk perception using flight initiation distance (FID) experiments with an approaching human observer and found that urban dwelling vervet monkeys (*Chlorocebus pygerythrus*) delayed fleeing from an approaching human compared with individuals found in rural areas. The authors presumed that this difference was related to potentially lethal conflict over crop-raiding in agricultural areas leading to heightened perceptions of risk (Mikula et al. 2018). Finally, five studies tested captive or wild predator-naïve primate populations for their predator recognition abilities (Cagni et al. 2011; Friant, Campbell, & Snowdon, 2008; Gil-da-Costa et al. 2003; Gil-da-Costa, 2007; Sündermann, Scheumann & Zimmermann, 2008). Results

from these studies suggest that predator recognition is sometimes innate but often requires learning about predators and their cues.

DISCUSSION

Although relatively little research uses primate antipredator behaviors for identifying when species are adversely affected by HIREC, we located a set of highly relevant studies focused on primate-predator interactions and antipredator behaviors. Their approaches included using antipredator behavior to gauge hunting pressure (Bshary 2001; Croes et al. 2007; Papworth, 2013), to investigate how primates deal with fear of (potentially lethal) conflict with humans (Bryson-Morrison et al. 2017; Fehlmann et al. 2017; Lindshield et al. 2017; Mikula et al. 2018), and/or to assess whether predator-naïve primates could discern whether an animal was dangerous (Cagni et al. 2011; Friant, Campbell, & Snowdon, 2008; Gil-da-Costa et al. 2003; Gil-da-Costa, 2007; Sündermann, Scheumann & Zimmermann, 2008). Data on primate habitat use and risk-sensitive behaviors were also used to assess whether perceived risk varied between more natural or human-modified habitats (Nowak et al. 2016a; 2017) and whether primates tended to avoid areas where native or exotic predators spent more time (Farris et al. 2014). Below we expand on the potential benefits and drawbacks of the various methods available for studying risk-sensitive behavior in primates with respect to understanding environmental change.

**Direct Observation of Habituated Subjects**

Habituation to observers and "human-shields" may compromise researchers' ability to assess how threats from humans or predators affect behavior and ecology of wild primate prey species. Researchers originally thought that this phenomenon was limited to humans deterring unhabituated predators rather than introducing behavioral changes in primate prey (Crofoot et al. 2010). However, evidence for a "human-shield" has been found in a variety of taxa (Atickem et

al. 2014; Berger 2007; Muhly et al. 2011; Nowak et al. 2014; Sarmento & Berger, 2017). How long this phenomenon persists likely depends on the types and tolerance of predator species present (Smith et al. 2018) and whether those individual predators tend to have negative or relatively neutral interactions with humans (Figure 2) (Isbell & Young, 1993). Additional issues with direct observation include researcher assumptions about which behaviors are sensitive to perceived predation risk. Studies of vigilance have been criticized because numerous social and environmental factors can affect the behavioral markers researchers tend to record (Allan & Hill, 2018; Stanford 2002; Treves 2000). While alarm calls may provide a more reliable indication of immediate risk perception, recorded spatial patterns may be relevant only when subjects are in proximity to observers. Finally, studies of anthropogenic risk focused on risk of conflict or of being hunted may also be biased because "behavioral spillover" could lead habituated primates to perceive potentially dangerous humans as less risky (Geffroy et al. 2015; Kasereka et al. 2006). Thus, we cannot assume that observer recorded patterns of risk-sensitive behavior will necessarily match up with the experience of unhabituated animals (Figure 1); the use of technologies and/or field experiments that do not require habituation may be preferable for most HIREC / conservation-related questions.

Notable exceptions to the problem of observer presence include studies of habituated chimpanzees hunting other primates (Stanford, 1995; Teelen, 2008; Watts & Amsler, 2013) and studies of carnivores that were tracked by observers (Zuberbühler, Jenny, & Bshary, 1999). These detailed observations have certainly advanced the study of primate-predator interactions. Yet, researchers should remain cautious about interpreting overall predation rates or spatial patterns of risk from these data. Previous studies have found that direct observation might affect how successful hunting chimpanzees are at killing prey species, if unhabituated prey alarm call

at approaching humans (Boesch, 1994). Conversely, if unhabituated prey associate humans with specific predators, they may learn to detect these cues earlier, leading to reduced hunting success. These studies are therefore useful for understanding basic behavioral ecology, but tracking predators likely has less utility for research on anthropogenic risk.

## Indirect and Remote Monitoring

### *Movement Data*

Monitoring movement through GPS or radio collars is now widely used in animal ecology (Kays et al., 2015) and has become more common for studying primate behavior and primate-predator interactions in recent years (Figure 3). While only one study reviewed used remotely monitored collar data to investigate how primates might respond to risk from humans (Felhmann et al. 2017), numerous questions about habitat alteration or anthropogenic effects on risk perception could be investigated with the help of these technologies. These might include investigations into how predator-primate movement and interaction frequency might differ between continuous vs. fragmented or degraded habitats. Location data can also be used to assess how human activity or infrastructure might alter space-use in both primates and their predators. Thus far, many studies have investigated similar questions in large carnivores (Ngoprasert et al. 2007; Ordiz et al., 2011; Van Cleave et al. 2018), but monitoring both predator and prey could indicate whether areas of high human activity function as “shields” for primates. This might especially be true where predators are subject to conflict or trophy hunting (Ordiz et al., 2011).

Employing similar methods in areas where primates are at risk from hunters could help explore how risk effects from human predation affect overall movement and whether subjects preferentially utilize locations and (micro)habitats further from human settlements. Coupling this with vegetation data on resource availability and habitat permeability to predict how

anthropogenic risk would influence movement or utilization would mimic studies of predator-induced “landscapes of fear” (Laundré et al. 2010; Willems and Hill, 2009) and would be novel for wild primates. In areas where hunting of primates is legal and hunters themselves are willing to assist researchers, information about hunter tactics and movements might also provide useful information for managers seeking to protect wild species through a better understanding of which microhabitats might serve as refuge from hunters. In a study of human movement ecology, Papworth et al. (2012) asked human subjects to carry handheld GPS devices during hunting and gathering activities and found that methods used for estimating habitat selection and resource use in wildlife could be effectively applied to humans. While the authors explicitly examined human behavior, similar methods could be used in conjunction with data from populations of wild primates already studied with GPS collars. A knowledge of where and when human-primate interactions tend to be lethal could inform managers about the types of habitats that are important for restoration or conservation and that could ensure more sustainable hunting. A final application of using remotely sensed movement data for measuring risk-sensitive behavior could be to assess observer effects on already studied populations to explore whether resource selection, landscape utilization, and activity patterns differ when groups are under continuous observation compared to periods with little or no proximity to researchers.

An important limitation of these methods is that they generally cannot estimate overall predation rates; researchers may underestimate the strength of antipredator behavior because encounters with uncollared predators (or humans not participating in a study) will go undetected. This can also be the case for encounters that occur between GPS fixes (Creel, Winnie, and Christianson, 2013) and for primate species living in multi-predator environments under risk from several predators simultaneously.

*Camera Trap Data*

Motion-sensitive camera traps are widely used for remotely collecting data on animal abundance and density and can provide estimates of co-occurrence between predators and prey. While much camera trap work focuses on estimating population sizes (Burton et al. 2015), they can be used for measuring behaviors such as temporal or spatial avoidance of competitors or of predators by prey (Farris et al. 2014; Niedballa et al. 2019). Although camera traps have typically been used on terrestrial wildlife, recent studies have validated their use at ground level for semi-terrestrial species (Cappelle et al. 2019) and, by placing cameras strategically along natural crossing points in forest strata, for arboreal primates (Gregory et al. 2014). In some instances, camera traps can provide data comparable to direct observation, including individual identities (McCarthy et al. 2019), as well as help researchers avoid the risks associated with habituating wild primates. For example, Boyer-Ontl and Pruetz (2014) used cameras to monitor cave use by unhabituated West African savannah chimpanzees. Their photos also indicated where chimpanzees and carnivores co-occurred on the landscape. Isbell and Bidner (2016) combined data from GPS-collared leopards and collared vervet monkeys with camera trap photographs to detect leopard visits to sleep sites. Future applications of these methods could include measuring primate occurrence data across a gradient of land types to determine whether areas of high human activity might serve as refuges from predators. Conversely, this approach could also be used to assess whether fear of human hunting is associated with landscape-level patterns of species occurrence. While we could not find any examples with primates, such studies have been conducted with other taxa (Muhly et al. 2011).

*Predator Diets*

Examining the hunting and dietary habits of the predators of primates is one way to study predation without human interference (Isbell 1994). Knowledge of a primate species' behaviors coupled with this information can be useful for assessing relative predation vulnerability between populations or species. Irwin et al. (2009) and Brockman et al. (2008) both used these methods for inferring whether HIREC could alter predation on wild lemurs by native carnivores (Irwin et al.) through habitat alteration and the introduction of exotic wild cats (*Felis silvestris*) (Brockman et al.). Prey remains within predator scat could be analyzed using morphological markers (e.g. hair cross sections, bones) or by extracting fDNA. Of the two methods, morphological markers are more commonly used to identify prey items and are relatively inexpensive, but molecular methods coupled with Sanger or more recently developed high-throughput sequencing (HTS) can help reduce uncertainty about both prey and predator identity (Monterroso et al. 2019). Future research should compare predator diet composition in areas with long-term research projects with nearby areas of similar community composition, but with relatively less human activity. This would provide needed information on whether spatial or temporal avoidance of humans might alter prey selection.

**Field Experiments**

*Cues from Hunters or Predators*

Three of the reviewed studies using field experiments with cues from human hunters found evidence that primates respond to these with antipredator behaviors (Bshary, 2001; Croes et al. 2007; Papworth et al. 2013). The major implication of this result is that behavioral indicators might also be used to identify populations in need of additional protection when it is uncertain whether hunting/poaching is occurring, and this information should help managers decide where to allocate resources for protection of large reserves or parks. Testing differences

between populations to responses to human presence, however, may be less useful if researchers make comparisons between unprotected areas and protected areas with high tourist or researcher activity. In these instances, researchers must be careful that the heightened "antipredator" behaviors they record in unprotected locations do not simply indicate a lack of experience with humans rather than differences in hunting/predation pressure. Nevertheless, there is evidence that some primates can distinguish between non-threatening and dangerous types of humans based on their behavior/appearance (Papworth, 2013). A new way of implementing these kinds of experiments is to couple camera traps with playback cues from hunters or predators using the Automated Behavioral Response system developed by Suraci et al. (2017). In their preliminary experiments, the authors successfully used speakers triggered by motion sensors to play sounds of human hunters at Bwindi Forest, Uganda, to gauge illegal hunting pressure without observer interference. This system has also allowed researchers studying cougar (*Puma concolor*) responses to anthropogenic sounds to measure whether fear of humans could alter their risk perception and predation behavior, resulting in a human-induced foraging cascade (Smith et al. 2017). This system could also be a powerful way of testing fear responses across a range of taxa going forward.

*Predator Recognition Experiments*

How primates acquire knowledge about and respond appropriately to predators is an important area of research because reintroductions and translocations can lead predator-naïve primates to encounter unfamiliar predators. This problem will likely be exacerbated by altered species distributions due to climate change (Estrada et al. 2017). Across taxonomic groups, failure to fully account for how naïve prey may be unable to recognize and react to predator cues has contributed to the failure of many releases from captive-breeding programs (Sinclair et al.

1998). This problem was an impetus for studies of predator recognition in captive-born, primate groups (Cagni et al. 2011; Friant et al. 2008; Sündermann et al. 2008) and studies of wild born but predator-naïve primates (Gil-da-Costa et al. 2003; Gil-da-Costa 2007). Prior identification of predator naïveté has allowed behavioral researchers to design methodologies for training captive prey pre-release (Moseby, Carthey, & Schroeder, 2015) or in-situ (West et al. 2018) to limit excessive mortality. For similarly inexperienced prey dealing with exotic predators, some evidence suggests that those that have historically had to avoid similar types of predators and have potentially evolved the ability to recognize certain cues or features as dangerous are at less risk of extinction (Ehlman, Trimmer, & Sih, 2019). Testing whether this is true for various species of wild primates should help predict which are likely able to cope with new or invasive predators in the future.

*Flight Initiation Distance*

While most unhabituated animals are intolerant to humans, flight distance can indicate relative differences in perceived risk. This can be used as an indirect measure of the degree of disturbance, conflict, or hunting affecting different populations or groups of the same species (Boer et al. 2004). These types of studies can be used for assessing how tourism in protected areas can lead to habituation or sensitization (Sutton and Heske, 2017). Increased flight distance over time or between populations can also indicate evidence for hunting/poaching or increased conflict (Donadio and Buskirk, 2006). Our literature search located only one primate FID study that focused on differences in vervet monkey FIDs between rural and urban settings and attempted to relate flight distance to group size, age-sex class, and habitat type (Mikula et al. 2018). Although valuable in highlighting the methodological approach, the study grouped data between sites without providing specific information on the relative danger from various threats

(e.g. conflict with humans, predators, hunting). Furthermore, unambiguous interpretations of the data were difficult because urban-dwelling groups were consistently smaller than their rural groups and potentially more tolerant to humans. Many other FID studies have similarly compared flight distances to an approaching observer between areas designated as "disturbed" and "undisturbed," without accounting for the possibility that individuals or groups that are naturally more tolerant or bold across a variety of taxa might be better able to exploit areas with greater human activity (Samia et al. 2015). For example, yellow-bellied marmots (*Marmota flaviventris*) with more consistent human disturbance had lower FIDs, indicating those individuals had become more tolerant of humans (Petelle et al. 2013). The authors attributed this difference to habituation or spatial assortment based on personality characteristics. Increased flight distances could also be due to decreased energy costs of initiating flight earlier due to more easily available forage in urban areas (Møller et al. 2015). The latter may often be the case with primates living in anthropogenic habitats because they are often able to exploit energy-rich anthropogenic food sources (Brennan, Else, & Altmann, 1985).

Although not included in the literature review, Allan, Bailey, and Hill (*In Review*) used FID methodology and found that individual habituated grey-footed chacma baboons (*P. u. griseipes*) likely perceived an approaching observer more as a social threat than a predator. The authors also found that tolerance to an approaching human was highly distinct amongst individuals, and repeatable within individuals, suggesting that the process of habituation does not result in equal tolerance to a stimulus across a social group. This suggests that habituated subjects may not be appropriate targets for FID studies of predation risk. While FID methods should be used by researchers aiming to measure how anthropogenic environmental change

affects risk-sensitivity, these methods are best applied when detailed information on both the study site location(s) and characteristics of the study subjects are well understood.

*Giving-up Densities*

Giving-up Density (GUD) methods have been used with wild primates to examine differences in perceived predation risk between microhabitats (Emerson et al. 2011; Makin et al. 2012) and risk from humans on foraging trade-offs (Nowak et al. 2016a, 2016b, and 2017). Nowak et al. (2014) used these methods with habituated animals and found that when not in proximity to an observer, individuals tended to forage less from the ground, suggesting the presence of a "human-shield." From a conservation standpoint, GUD experiments are likely to be most useful when they can serve as an indicator of habitat selection in anthropogenically-altered environments in which human activity might alter food availability, predator density, or habitat structure (Bleicher, 2017). For example, GUDs have been used in non-primate taxa to assess which habitats serve as refuges (Carter & Bright, 2003) and to contrast foraging behavior in fragmented or degraded habitats with more pristine environments (Whelan & Jedlicka, 2007). However, GUDs have been criticized as a relatively coarse indicator of habitat quality because a high GUD can indicate a both resource-rich environment and an area of high perceived predation risk. Thus, environment-specific attributes such as food availability or predator density need to be accounted between patch locations (Brown, 1988). An additional factor is that in social species, multiple individuals may access the same patch simultaneously. To avoid results being driven by bolder and/or more risk-insensitive individuals, patches should be spread out to reduce monopolization (Réale & Festa-Bianchet, 2003). Non-target species may also feed from artificial patches, but this might be overcome by introducing the setup to target animals in stages, allowing them to learn that patches contain food while slowly increasing the complexity of the

design. Furthermore, using camera traps or animal-triggered video cameras in place of direct observation could help remove potential "human-shield" bias (Bedoya-Perez et al. 2013; Emerson et al. 2011; Nowak et al. 2014).

## CONCLUSIONS

Global change is relevant to behavioral biology because many long-term field sites focused on the adaptive significance of behavior will likely be compromised by extensive environmental change (Caro & Sherman, 2011), and this includes long-term studies of primates (Hockings et al. 2015). While much of the order's inherent behavioral flexibility may help certain species survive alongside humans (McLennan, Spagnoletti, and Hockings, 2017), the environments encountered in the next century may be very different from those that most living species experienced over the course of their evolution (Hockings et al. 2015). Among these changes, numerous examples indicate that human activities can alter natural predator-primate relationships.

Each method reviewed here has inherent benefits and drawbacks that are likely to vary between specific study species, populations, and habitats. Direct observation of risk-sensitive behaviors may be the most logistically workable method for a wide range of primate researchers, but it does not necessarily produce ecologically realistic results. The alternative methodologies we discuss here will often constrain the types of questions researchers can ask and provide less detail about individual subjects, but likely provide more accurate data on predator-primate relationships. Given what we currently know about the ways in which humans can impact primate risk perception, we believe these alternatives can benefit both basic primate behavioral ecology and ultimately contribute to species conservation.

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Tables

Table 1. Methods of monitoring antipredator behaviors and primate-predator interactions used in reviewed studies for investigating HIREC or species conservation

| Topic / Concern | Method of Investigation | Citation |
|---|---|---|
| Anthropogenic influences on risk perception (hunting, human-shields, conflict with humans) | Field Experiments - visual/auditory cues from humans | Bshary (2001); Croes et al. (2007); Papworth et al. (2013) |
| | Field Experiments - giving-up densities | Nowak et al. (2014); (2016a); (2016b); (2017) |
| | GPS/movement data | Fehlmann et al. (2017) |
| | Observation of risk-sensitive behaviors | Bryson-Morrison et al. (2017); Lindshield et al. (2017) |
| | Field Experiments - flight initiation distance | Mikula et al. (2018) |
| Over-predation or alteration to predation rates (invasive predators, altered habitat) | Predator diets (scat or known kills) | Brockman et al. (2008); Irwin et al. (2009) |
| | Camera traps - co-occurrence or spatial/temporal avoidance of predators | Farris et al. (2014) |
| | Direct observation of habituated predators | Teelen (2008); Watts & Amsler (2013) |
| Predator recognition abilities (reintroduction or translocation of primates or predators) | Field Experiments - real or simulated cues from potential predators | Cagni et al. (2011); Friant, Campbell, and Snowdon (2008); Gil-da-Costa et al. (2003); Gil-da-Costa (2007); Sündermann et al. (2008) |

1

**Figure legends**

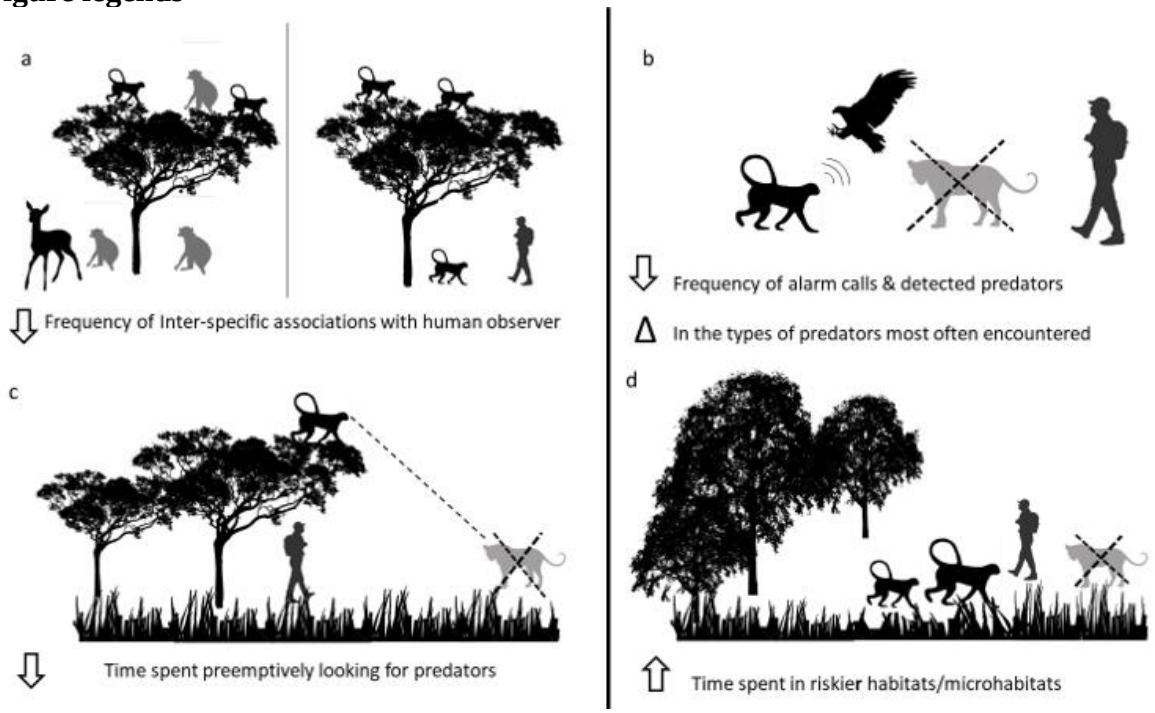


**Figure 1. Predicted effects of human presence/direct observation on primate groups.** (a) Human presence with habituated wildlife may produce changes in the types of species encountered and changes from pre-habituation levels of inter-species association patterns when differences in habituation exist between species (different colors and shapes represent different species). (b) Certain guilds of predators may be more intolerant than others resulting in potentially erroneous conclusions about the importance of certain predators for a primate species ecology. (c) Over time, decreased predator encounter rates while with human observers could lead to decreased wariness and less time spent looking for predators. (d) Time spent in riskier habitats while under observation may also increase if subjects perceive themselves to be safer while in proximity to an observer.

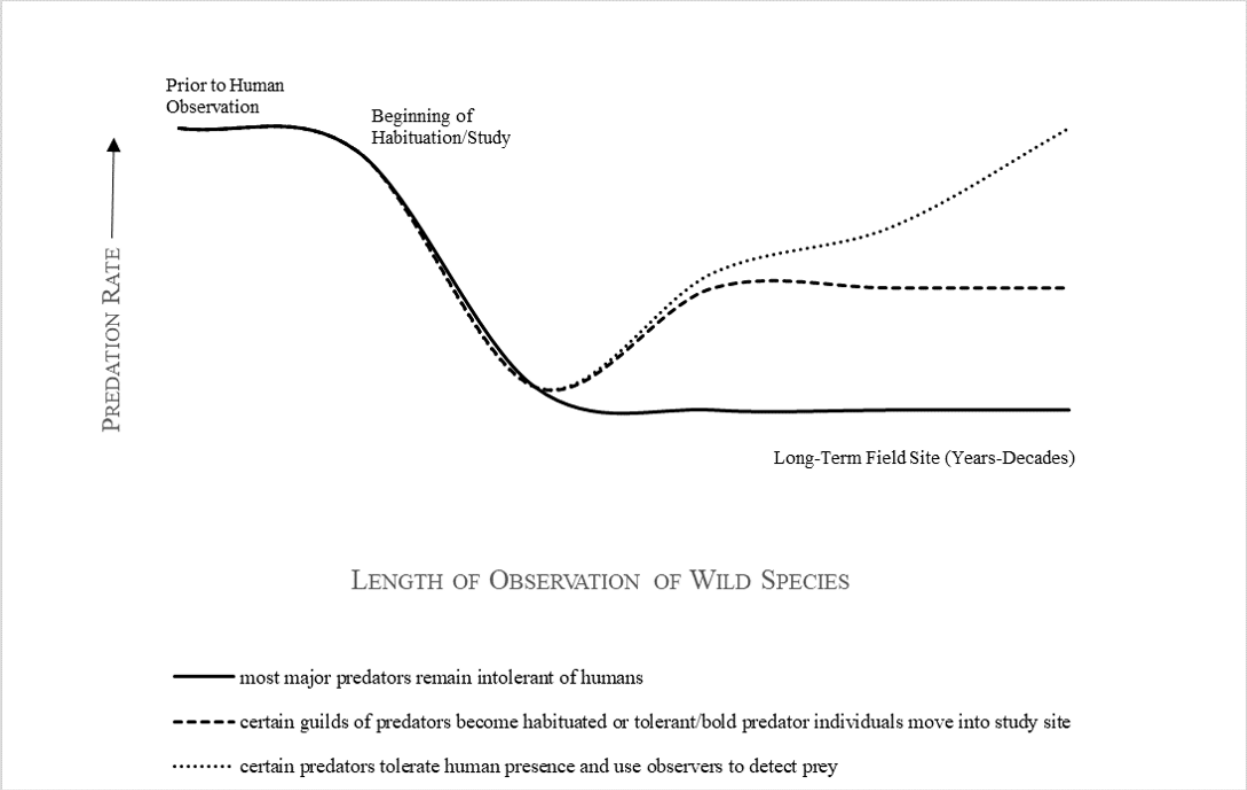


**Figure 2. Hypothetical effects of direct observation on predation rates of habituated primate groups.** Predators may remain intolerant of researchers for the duration of study and avoid hunting individuals within a habituated study group. Certain guilds may become more habituated to human presence over time or bolder individuals that are more tolerant of people may eventually move into a study location. This may be less likely to occur if predator species are under hunting pressure from humans.

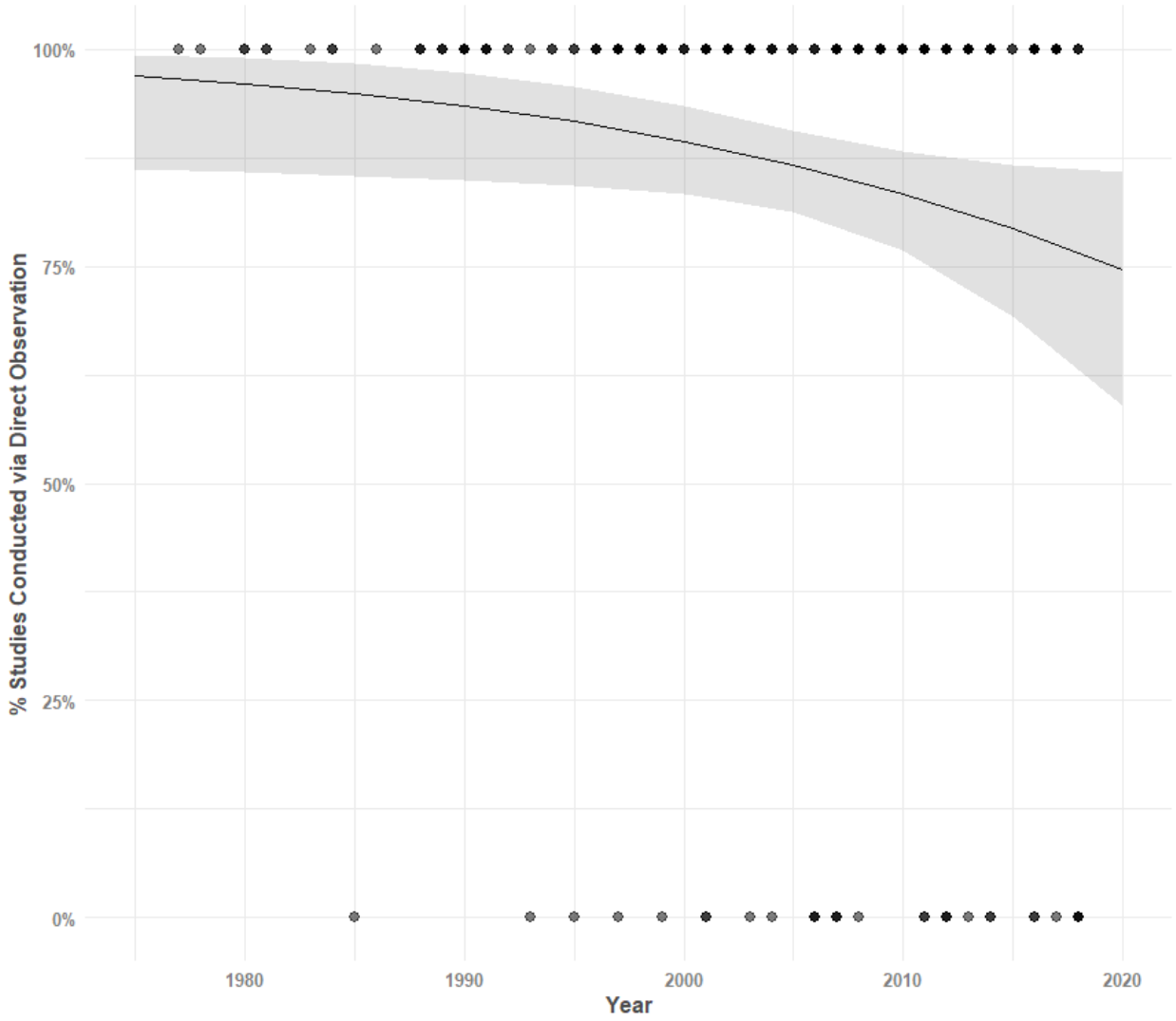


**Figure 3. Percentage of sampled studies using direct observation of habituated subjects over the sampled years.** We found the incidence of articles using direct observation slightly declined over time ($\beta = -0.0442$, SE = $\pm 0.0246$) using a binomial model adjusted for varying numbers of sampled articles per year.

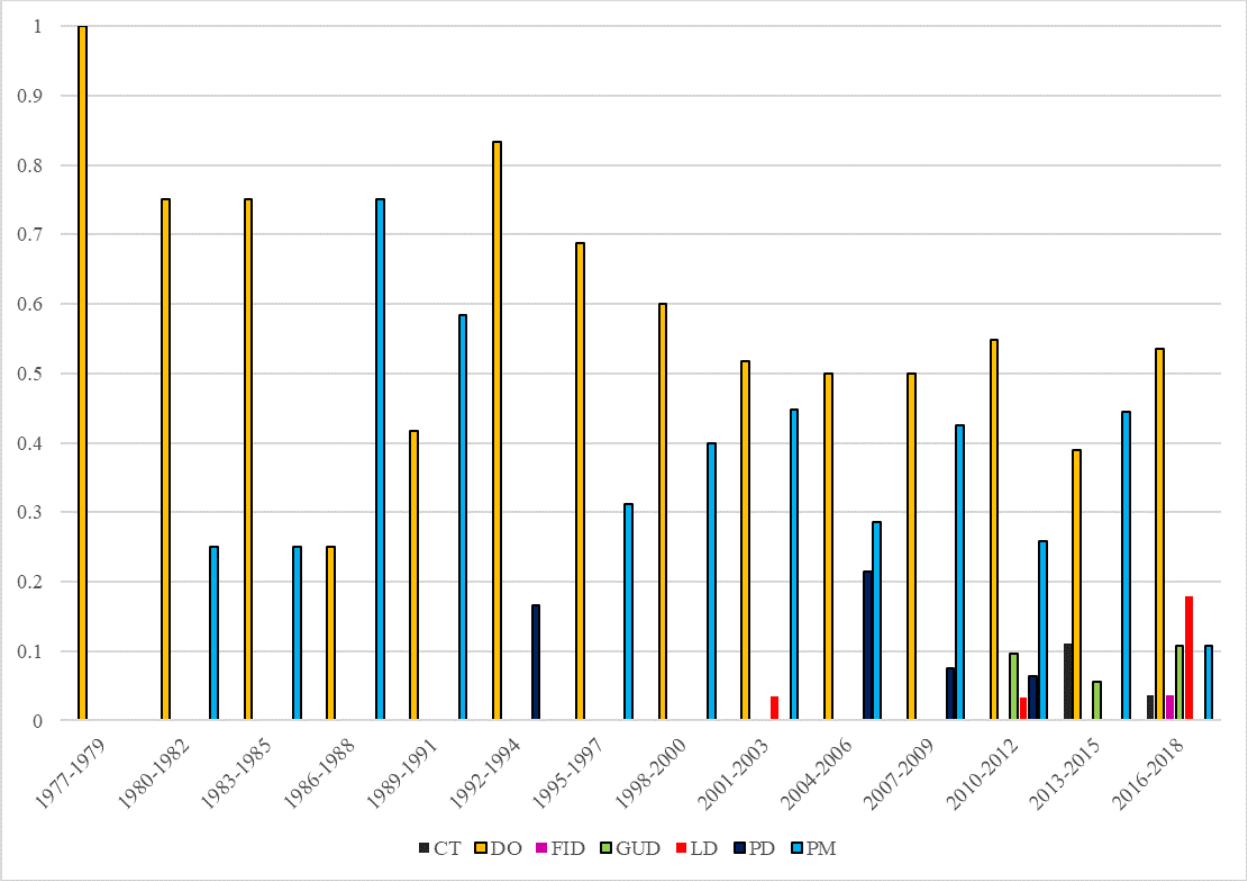


**Figure 4. Proportion of studies using reviewed methods.** CT is camera trapping, DO is direct observation, FID is flight initiation distance experiment, GUD is giving-up density experiment, LD is remotely sensed movement data from radio or GPS collars, PD is predator diet information, and PM is experiments using predator/hunter sensory cues.